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A System of Resource-Based Growth Models with Two Resources in the Unstirred Chemostat[1]

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Models of single-species growth in the unstirred chemostat on two growth-limiting, nonreproducing resources are considered. For the case of two complementary resources, the existence and uniqueness of a positive steady-state solution is established. It is also proved that the unique positive solution is globally attracting for the system with regard to nontrivial nonnegative initial values. For the case of two substitutable resources, the existence of a positive steady-state solution is determined for a range of the parameter (m, n). Techniques include the maximum principle, monotone method and global bifurcation theory. The longtime behavior of the corresponding limiting system is given for a range of (m, n). In the special case of $m = n$, the uniqueness and global attractivity of the positive steady-state solution of the original system is established. © 2001 Academic Press

Key Words: chemostat; steady-state solution; maximum principle; global attractivity; global bifurcation.

1. INTRODUCTION

The chemostat is a laboratory apparatus used for the continuous culture of microorganisms. Mathematical models of the chemostat are surprisingly amenable to analysis. Predictions based on parameters in the model that can be measured have been tested experimentally and outcomes have been shown to agree rather well with the theory [1].

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In the basic set-up, one or more populations of microorganisms grow and/or compete in a well-stirred culture vessel for a single nutrient that is supplied at a constant rate, at a growth-limiting concentration. The contents of the culture vessel are removed at the same constant rate so that the volume of the culture vessel is kept constant. When more than one resource is limiting, it is necessary to consider how the resources, once consumed, promote growth. At one extreme are resources that are sources of different essential substances that must be taken together, because each substance fulfils different physiological needs with respect to growth, for example, a carbon source and a nitrogen source. Such resources are called complementary by Leon and Tumpson [2], Rapport [3], and Baltzis and Fredrickson [4], essential by Tilman [5] and heterologous by Harder and Dijkhuizen [6].

On the other hand, alternative sources of an essential substance, or substances that fulfil the same physiological needs, such as two carbon sources or two nitrogen sources, are called perfectly substitutable by Leon and Tumpson [2], Rapport [3], Tilman [5] and homologous by Harder and Dijkhuizen [6]. For an excellent survey of the experimental literature in both of these cases, see Egli [7].

In this paper, we discuss these two extreme cases in the unstirred chemostat. If $S(t)$, $R(t)$ denote the nutrient concentrations at time t and $u(t)$ is the biomass of the population in the culture vessel, then the well-stirred complementary model is given by

$$S_t = (S^0 - S)\,D - \frac{1}{y_S}\,h(S, R)\,u,$$

$$R_t = (R^0 - R)\,D - \frac{1}{y_R}\,h(S, R)\,u,$$

$$u_t = [-D + h(S, R)]\,u,$$

where $S^0 > 0$ and $R^0 > 0$ are constants, that represent the input concentrations of nutrients S and R respectively, and D is the dilution rate, y_S and y_R are the corresponding growth yield constants. We denote the response function by $h(S, R) = \min(m_1 S/(a_1 + S), n_1 R/(b_1 + R))$, where m_1, n_1, a_1, b_1 are positive constants. This model can be thought of as the submodel treated in Ref. [8]. They assume that the consumption rate of the resources follows Type II functional response, or equivalently Michaelis–Menten kinetics, generalized to the two complementary resources case.

The well-stirred substitutable model is given by the following differential equations

$$
\begin{aligned}
S_t &= (S^0 - S)\,D - \frac{m}{y_S}\,uf(S, R),\\
R_t &= (R^0 - R)\,D - \frac{n}{y_R}\,ug(S, R),\\
u_t &= [-D + mf(S, R) + ng(S, R)]\,u,
\end{aligned}
$$

where $m = m_S/K_S$, $n = m_R/K_R$, and the response functions are a generalization of the familiar Michaelis–Menten prototype of functional response for a single resource in Ref. [9], and given by

$$
f(S, R) = \frac{S}{1 + \frac{1}{K_S}S + \frac{1}{K_R}R} \triangleq \frac{S}{1 + aS + bR},
$$

$$
g(S, R) = \frac{R}{1 + \frac{1}{K_S}S + \frac{1}{K_R}R} \triangleq \frac{R}{1 + aS + bR}.
$$

Here $m_S > 0$ is the maximal growth rate of species u on resource S in the absence of resource R, and $K_S > 0$ is the corresponding half-saturation constant. The constants $m_R > 0$ and $K_R > 0$ are defined similarly. The motivation for this model is given in Ref. [10].

Mathematical work on chemostat models involving two limiting resources under the "well-stirred" condition can be found in, for example [8–12] and the references therein.

In the current paper, we remove the "well-stirred" hypothesis of the basic chemostat, and consider the unstirred chemostat with two growth-limiting, nonreproducing resources. Just as for the unstirred chemostat with one resource in Refs. [13–22], the systems are taken as the following form of reaction-diffusion equations: complementary and substitutable case, respectively,

$$
\begin{aligned}
S_t &= dS_{xx} - \frac{1}{y_S}\,uh(S, R),\\
R_t &= dR_{xx} - \frac{1}{y_R}\,uh(S, R), \qquad 0 < x < 1,\\
u_t &= du_{xx} + uh(S, R);\\
S_t &= dS_{xx} - \frac{m}{y_S}\,uf(S, R),
\end{aligned}
$$

$$R_t = dR_{xx} - \frac{n}{y_R} ug(S, R), \qquad 0 < x < 1,$$

$$u_t = du_{xx} + u(mf(S, R) + ng(S, R))$$

with boundary conditions

$$\begin{aligned} &S_x(0, t) = -S^0, && R_x(0, t) = -R^0, u_x(0, t) = 0, \\ &S_x(1, t) + \gamma S(1, t) = 0, && R_x(1, t) + \gamma R(1, t) = 0, \\ &u_x(1, t) + \gamma u(1, t) = 0. \end{aligned}$$

The boundary conditions are very intuitive and appropriate for this type of equations. The interested reader may refer to Refs. [13–15] for their derivation and some explanation in the case of the unstirred chemostat with one resource.

These equations are simplified using nondimensional variables and parameters, which are defined below: $\bar{S} = S/S^0$, $\bar{R} = R/R^0$, $\rho = y_S S^0/y_R R^0$, $\bar{a}_1 = a_1/S^0$, $\bar{b}_1 = b_1/R^0$, $\bar{h}(\bar{S}, \bar{R}) = \min(m_1 \bar{S}/(\bar{a}_1 + \bar{S}), n_1 \bar{R}/(\bar{b}_1 + \bar{R}))$, $\bar{a} = aS^0$, $\bar{b} = bR^0$, $\bar{m} = mS^0$, $\bar{n} = ny_S S^0/y_R$, $c = y_R R^0/y_S S^0$, and $\bar{u} = u/y_S S^0$. In order to save notation, we drop the overbars on the nondimensional variables and parameters. In the scaled form, we have the following equations corresponding to the complementary and substitutable cases, respectively,

$$\begin{aligned} &S_t = dS_{xx} - uh(S, R), \\ &R_t = dR_{xx} - \rho uh(S, R), \qquad 0 < x < 1, \\ &u_t = du_{xx} + uh(S, R); \end{aligned} \tag{1.1}$$

$$\begin{aligned} &S_t = dS_{xx} - muf(S, R), \\ &R_t = dR_{xx} - nug(S, R), \qquad 0 < x < 1, \\ &u_t = du_{xx} + u(mf(S, R) + cng(S, R)) \end{aligned} \tag{1.2}$$

with boundary conditions

$$\begin{aligned} &S_x(0, t) = -1, && R_x(0, t) = -1, \qquad u_x(0, t) = 0, \\ &S_x(1, t) + \gamma S(1, t) = 0, && R_x(1, t) + \gamma R(1, t) = 0, \\ &u_x(1, t) + \gamma u(1, t) = 0 \end{aligned} \tag{1.3}$$

and initial conditions

$$S(x, 0) = S_0(x) \geqslant 0, \qquad R(x, 0) = R_0(x) \geqslant 0, \qquad u(x, 0) = u_0(x) \geqslant 0, \ \not\equiv 0. \tag{1.4}$$

As noted above, the unstirred chemostat with one resource has been considered by many authors in the past decade. Just as pointed out in Ref. [13], the unstirred chemostat with two resources is more realistic and thus of interest. The present paper is devoted to determining the positive solution and longtime behavior of the models of the unstirred chemostat with two resources and one species. In the complementary case (1.1), we obtain a critical value $\lambda_0' > 0$, given by the principal eigenvalue problem (2.4) below. Washout of the species from the chemostat occurs if $\lambda_0' > 1$; uniqueness and global attractivity of the positive steady-state solution occurs if $\lambda_0' < 1$. In the substitutable case, the result seems more complicated. We try to distinguish the existence of the steady-state solution in the parameter ranges of (m, n). It is shown that there is only the washout solution of (1.2) if $\max(m, n) \leqslant \lambda_0/(1+c)$, where λ_0 is defined in (3.6) below as the principal eigenvalue. The existence of a positive steady-state solution is proved by using the monotone method if $\min(m, n) > \lambda_0/(1+c)$ or either of the following holds: $m > \lambda_0$, $n \leqslant \lambda_0/(1+c)$ or $m \leqslant \lambda_0/(1+c)$, $n > \lambda_0/c$. The situation for the remaining part of (m, n) is more delicate. Under certain conditions, it is proved that, in this range, there is only the washout solution if $m + cn \leqslant \lambda_0$; and there is a positive steady-state solution if $m + cn > \lambda_0$. The longtime behavior of the limiting system is also discussed in the conclusion. Since the limiting system is of inhomogeneous boundary conditions, it is more difficult to treat than in the case of one resource. A delicate estimate is needed, which is closely dependent on the particular form of the response functions.

The paper is set up as follows. In Section 2, we focus on the complementary case (1.1). The existence and attractivity of a positive steady-state solution is fully established by using the Maximum Principle and L^p estimate for elliptic equation. In Section 3, we consider the substitutable case. The existence of a positive steady-state solution of (1.2) is obtained by the quasi-monotone method and global bifurcation theory. The longtime behavior of the corresponding limiting system is also given for a range of (m, n).

2. THE COMPLEMENTARY CASE

First, we consider the corresponding steady-state system of (1.1)

$$\begin{aligned} &dS_{xx} - uh(S, R) = 0, \\ &dR_{xx} - \rho uh(S, R) = 0, \qquad 0 < x < 1, \\ &du_{xx} + uh(S, R) = 0 \end{aligned} \tag{2.1}$$

with boundary conditions

$$\begin{array}{lll} S_x(0) = -1, & R_x(0) = -1, & u_x(0) = 0, \\ S_x(1) + \gamma S(1) = 0, & R_x(1) + \gamma R(1) = 0, & u_x(1) + \gamma u(1) = 0. \end{array} \tag{2.2}$$

It follows that $S + u = z$, $R + \rho u = z$, where $z = z(x) = \frac{1+\gamma}{\gamma} - x$. Then u satisfies

$$\begin{gathered} du_{xx} + uh(z - u, z - \rho u) = 0, \qquad 0 < x < 1, \\ u_x(0) = 0, \qquad u_x(1) + \gamma u(1) = 0. \end{gathered} \tag{2.3}$$

Let λ_0' be the principal eigenvalue of the following problem, and $\phi'(x) > 0$ on $[0, 1]$ be the corresponding eigenfunction, normalized as $\max_{x \in [0, 1]} \phi'(x) = 1$

$$d\phi'_{xx} + \lambda_0' \phi' h(z, z) = 0, \qquad 0 < x < 1, \qquad \phi'_x(0) = 0, \qquad \phi'_x(1) + \gamma \phi'(1) = 0. \tag{2.4}$$

The proof of the following Lemmas 2.1–2.4 is quite usual and omitted here. The reader may refer to Refs. [15, 16, 22].

The following result shows that if $\lambda_0' \geqslant 1$, the unique nontrivial non-negative solution of (2.1)(2.2) is the washout solution $(z, z, 0)$.

LEMMA 2.1. *Suppose $\lambda_0' \geqslant 1$. Then $u = 0$ is the unique nonnegative solution of* (2.3).

Since we are concerned with nonnegative solutions (S, R, u) of (2.1), we redefine the response function as follows: $h(S, R) = \min(\bar{p}(S), \bar{q}(R))$, where

$$\bar{p}(S) = \begin{cases} p(S), & S \geqslant 0, \\ \tan^{-1}\left(\dfrac{2m_1 S}{a_1} + 1\right) - \dfrac{\pi}{4}, & S < 0, \end{cases}$$

$$\bar{q}(R) = \begin{cases} q(R), & R \geqslant 0, \\ \tan^{-1}\left(\dfrac{2n_1 R}{b_1} + 1\right) - \dfrac{\pi}{4}, & R < 0. \end{cases}$$

It is easily seen that $\bar{p}, \bar{q} \in C^1(-\infty, +\infty)$.

The following lemma shows that if u is a nontrivial nonnegative solution of (2.3), then $(z - u, z - \rho u, u)$ is really a positive solution of (2.1).

LEMMA 2.2. *Suppose that* u *is a nontrival nonnegative solution of* (2.3). *Then* $0<u<\min(1, 1/\rho)\, z(x)$.

If $\lambda_0'<1$, (2.1) has a unique positive solution, denoted by $(\hat{S}, \hat{R}, \hat{u}) = (z-\hat{u}, z-\rho\hat{u}, \hat{u})$, where $\hat{u}$ is defined in the following lemma.

LEMMA 2.3. *Suppose* $\lambda_0'<1$. *Then there exists a unique positive solution of* (2.3), *denoted by* $\hat{u}$.

The following lemma gives a condition under which the organism cannot survive in the given environment.

LEMMA 2.4. *If* $\lambda_0'>1$, *then the solution* (S, R, u) *of* (1.1) *satisfies*

$$\lim_{t\to\infty}(S, R, u) = (z, z, 0).$$

From system (1.1) it follows that $S(x,t)+u(x,t)=\varphi_1(x,t)$, $R(x,t)+\rho u(x,t)=\varphi_2(x,t)$, where $\varphi_i(x,t)$, $i=1,2$, is the unique solution of the following problem

$$\begin{aligned} &\varphi_{it} = d\varphi_{ixx}, && 0<x<1, \quad t>0,\\ &\varphi_{ix}(0,t) = -1, \qquad \varphi_{ix}(1,t)+\gamma\varphi_i(1,t)=0, && t>0,\\ &\varphi_i(x,0)=\varphi_{i0}(x), && 1<x<1, \end{aligned}$$

where $\varphi_{10}=S_0+u_0$, $\varphi_{20}=R_0+\rho u_0$.

If $\lambda_0'<1$, the unique positive solution $(\hat{S}, \hat{R}, \hat{u})$ is globally attracting. More precisely, we have

THEOREM 2.5. *If* $\lambda_0'<1$, *then* $\lim_{t\to\infty} u(x,t)=\hat{u}$, *where* $u(x,t)$ *is the solution of* (2.5).

Proof. Since $\lim_{t\to\infty}\varphi_i(x,t)=z(x)$ and $z(x)\geqslant\frac{1}{\gamma}$, we know that, with minor modification if necessary, for small $\varepsilon>0$, there exists $T>0$ such that $z-\varepsilon z<\varphi_i<z+\varepsilon$ for $x\in[0,1]$, $t\geqslant T$. This also implies that $u(x,t)\leqslant(z+\varepsilon)\min(1,\frac{1}{\rho})$ for $t\geqslant T$. By the Comparison Theorem for the parabolic equation we have

$$u_1(x,t)\leqslant u(x,t)\leqslant u_2(x,t) \qquad \text{for} \quad x\in[0,1], \quad t\geqslant T,$$

where $u_i(x, t)$, $i=1, 2$, are the solutions of the following problems respectively,

$$
\begin{aligned}
&u_{1t} = du_{1xx} + u_1 h(z - \varepsilon z - u_1, z - \varepsilon z - \rho u_1), && x \in (0, 1), \quad t > T,\\
&u_{1x}(0, t) = 0, \qquad u_{1x}(1, t) + \gamma u_1(1, t) = 0, && t > T,\\
&u_1(x, T) = \min(u(x, T), (z - \varepsilon z) \min(1, \tfrac{1}{\rho})), && x \in (0, 1);\\
&u_{2t} = du_{2xx} + u_2 h(z + \varepsilon - u_2, z + \varepsilon - \rho u_2), && x \in (0, 1), \quad t > T,\\
&u_{2x}(0, t) = 0, \qquad u_{2x}(1, t) + \gamma u_2(1, t) = 0, && t > T,\\
&u_2(x, T) = u(x, T), && x \in (0, 1).
\end{aligned}
$$

Now we are in a position to prove

$$
\lim_{t \to \infty} u_i(x, t) = u_i^\varepsilon(x), \qquad i = 1, 2, \tag{2.5}
$$

where $u_i^\varepsilon(x)$, $i=1, 2$, are the unique positive steady-state solutions of the following problems, respectively

$$
\begin{aligned}
du^\varepsilon_{1xx} + u^\varepsilon_1 \, h(z - \varepsilon z - u^\varepsilon_1, z - \varepsilon z - \rho u^\varepsilon_1) = 0,\\
u^\varepsilon_{1x}(0) = 0, \qquad u^\varepsilon_{1x}(1) + \gamma u^\varepsilon_1(1) = 0;
\end{aligned}
$$

and

$$
\begin{aligned}
du^\varepsilon_{2xx} + u^\varepsilon_2 \, h(z + \varepsilon - u^\varepsilon_2, z + \varepsilon - \rho u^\varepsilon_2) = 0,\\
u^\varepsilon_{2x}(0) = 0, \qquad u^\varepsilon_{2x}(1) + \gamma u^\varepsilon_2(1) = 0.
\end{aligned}
$$

Since $\lambda_0' < 1$, it follows that the principal eigenvalue $\lambda_\varepsilon' < 1$, in the problem below.

$$
\begin{aligned}
d\phi_{xx} + \lambda_\varepsilon' h(z + \varepsilon, z + \varepsilon)\, \phi = 0,\\
\phi_x(0) = 0, \qquad \phi_x(1) + \gamma \phi(1) = 0.
\end{aligned}
$$

Let ε be sufficiently small such that the principal eigenvalue $\lambda_\varepsilon'' < 1$ holds in the problem below.

$$
\begin{aligned}
d\phi_{xx} + \lambda_\varepsilon'' h(z - \varepsilon z, z - \varepsilon z)\, \phi = 0,\\
\phi_x(0) = 0, \qquad \phi_x(1) + \gamma \phi(1) = 0.
\end{aligned}
$$

We can proceed as in the proof of Lemma 2.2–2.3 to obtain the existence and uniqueness of $u_i^\varepsilon(x)$, $i=1, 2$, and

$$0<u_1^\varepsilon(x)<(z-\varepsilon z)\min\left(1, \frac{1}{\rho}\right), \qquad 0<u_2^\varepsilon(x)<(z+\varepsilon)\min\left(1, \frac{1}{\rho}\right).$$

Using a similar method as in Ref. [24], we can show that (2.5) holds.

In the following, we are going to show that

$$\lim_{\varepsilon\to 0} u_i^\varepsilon(x)=\hat{u}, \qquad i=1, 2. \tag{2.6}$$

Since $0<\delta\phi\leqslant u_1^\varepsilon(x)<(z-\varepsilon z)\min(1, \frac{1}{\rho})$, there exists a constant $K>0$, independent of ε, such that for any $p\geqslant 1$,

$$\|u_1^\varepsilon\|_{2, p}\leqslant K'(\|u_1^\varepsilon\|_p+\|u_1^\varepsilon h(z-\varepsilon z-u_1^\varepsilon, z-\varepsilon z-\rho u_1^\varepsilon)\|_p)\leqslant K.$$

By the Sobolev Embedding Theorem, using a subsequence if necessary, we know that $u_1^\varepsilon\to u_1^0$ in C^1 as $\varepsilon\to 0$, and $0<u_1^0\leqslant z\min(1, \frac{1}{\rho})$. Moreover, u_1^0 satisfies the following problem weakly

$$du_{1xx}^0+u_1^0 h(z-u_1^0, z-\rho u_1^0)=0,$$
$$u_{1x}^0(0)=0, \qquad u_{1x}^0(1)+\gamma u_1^0(1)=0.$$

Regularity of the elliptic equation leads to $u_1^0\in C^2$. Hence the uniqueness of $\hat{u}$ implies $u_1^0=\hat{u}$. This proves (2.6) for $i=1$. Similarly we can prove that (2.6) is valid for $i=2$.

By a combination of (2.5)(2.6) and the Comparison Theorem, we obtain $\lim_{t\to\infty} u(x, t)=\hat{u}$.

3. THE SUBSTITUTABLE CASE

In this section, we begin to treat the unstirred chemostat with two substitutable resources. Consider the steady-state system of (1.2)(1.3)

$$\begin{aligned} dS_{xx}-muf(S, R)&=0,\\ dR_{xx}-nug(S, R)&=0,\\ du_{xx}+u(mf(S, R)+cng(S, R))&=0 \end{aligned} \tag{3.1}$$

with boundary conditions

$$\begin{array}{lll} S_x(0) = -1, & R_x(0) = -1, & u_x(0) = 0, \\ S_x(1) + \gamma S(1) = 0, & R_x(1) + \gamma R(1) = 0, & u_x(1) + \gamma u(1) = 0. \end{array} \tag{3.2}$$

First we give some estimates about the nonnegative solution of (3.1)(3.2). The similar proof can be found in Refs. [13, 22] and is omitted here.

LEMMA 3.1. *Suppose that* (S, R, u) *is a nonnegative solution of* (3.1)(3.2). *Then* $S > 0$, $R > 0$, *and either* $0 < S < z$, $0 < R < z$ *or* $S = R = z$. *Furthermore,* $S + cR + u = (1 + c)z$, *where* z *is defined in Section* 2.

Let $s = z - S$, $r = z - R$. Then by Lemma 3.1, either $0 < s$, $r < z$ or $s = r = 0$, and

$$\begin{aligned} ds_{xx} + m(s + cr)\, f(z - s, z - r) = 0, \\ dr_{xx} + n(s + cr)\, g(z - s, z - r) = 0 \end{aligned} \tag{3.3}$$

with boundary conditions

$$\begin{array}{ll} s_x(0) = 0, & r_x(0) = 0, \\ s_x(1) + \gamma s(1) = 0, & r_x(1) + \gamma r(1) = 0. \end{array} \tag{3.4}$$

3.1. *The Special Case of* $m = n$

In this subsection, we consider the case of $m = n$ and discuss the existence of a positive solution of (3.3) (or (3.1)) and its dynamics.

Let $w = s - r$. Then w satisfies

$$dw_{xx} - C(x)\, w = 0, \quad 0 < x < 1; \qquad w_x(0) = 0, \qquad w_x(1) + \gamma w(1) = 0,$$

where $C(x) = m(s + cr)/(1 + a(z - s) + b(z - r))$. It follows from the Maximum Principle that $w = 0$, which leads to $s = r$ on $[0, 1]$. Substituting into (3.3), we have

$$\begin{aligned} ds_{xx} + m(1 + c)\, sf(z - s, z - s) = 0, \\ s_x(0) = 0, \qquad s_x(1) + \gamma s(1) = 0. \end{aligned} \tag{3.5}$$

Let $\lambda_0 > 0$ and $\phi > 0$ be the principal eigenvalue and eigenfunction of the following problem, with ϕ normalized so that $\int_0^1 f(z, z)\, \phi^2\, dx = 1$,

$$\begin{aligned} d\phi_{xx} + \lambda_0\, f(z, z)\, \phi = 0, \\ \phi_x(0) = 0, \qquad \phi_x(1) + \gamma\phi(1) = 0. \end{aligned} \tag{3.6}$$

The result in Refs. [21, 22] leads to

THEOREM 3.2. *There exists a unique positive solution* $\hat{s}$ *of* (3.5), *if and only if* $m > m_0 \triangleq \lambda_0/(1+c)$. *Moreover* $0 < \hat{s} < z$, $\hat{s}$ *is continuous with respect to* $m \in [m_0, \infty)$, *and* $\lim_{m \to m_0+} \hat{s} = 0$ *uniformly in* $(0, 1)$, $\lim_{m \to \infty} \hat{s} = z$ *a.e.* $x \in (0, 1)$.

Remark 1. If $m > m_0$, then $(\hat{S}, \hat{R}, \hat{u}) = (z - \hat{s}, z - \hat{s}, (1+c)\,\hat{s})$ is the unique positive steady-state solution of (1.2) in the case of $m = n$.

Now we restrict our attention to the dynamics of (1.2).

THEOREM 3.3. *Suppose* $m = n$. *If* $m < m_0$, *then the solution* (S, R, u) *of* (1.2)–(1.4) *satisfies*

$$\lim_{t \to \infty} S(x, t) = z, \qquad \lim_{t \to \infty} R(x, t) = z, \qquad \lim_{t \to \infty} u(x, t) = 0.$$

If $m > m_0$, *then*

$$\lim_{t \to \infty} S(x, t) = z - \hat{s}, \qquad \lim_{t \to \infty} R(x, t) = z - \hat{s}, \qquad \lim_{t \to \infty} u(x, t) = (1+c)\,\hat{s}.$$

Proof. It follows from (1.2) that $S(x, t) + cR(x, t) + u(x, t) = (1+c)\,\varphi(x, t)$, where $\varphi(x, t)$ is the solution of

$$\begin{gathered} \varphi_t = d\varphi_{xx}, \\ \varphi_x(0, t) = -1, \qquad \varphi_x(1, t) + \gamma\varphi(1, t) = 0, \\ \varphi(x, 0) = \varphi_0(x) = \frac{S_0 + cR_0 + u_0}{1+c}. \end{gathered}$$

As before, we have

$$\lim_{t \to \infty} \varphi(x, t) = z \qquad \text{uniformly in } [0, 1]. \tag{3.7}$$

Let $w(x, t) = S(x, t) - R(x, t)$. Then

$$\begin{gathered} w_t = dw_{xx} - C(x, t)\, w, \\ w_x(0, t) = 0, \qquad w_x(1, t) + \gamma w(1, t) = 0, \\ w(x, 0) = w_0(x) = S_0(x) - R_0(x), \end{gathered}$$

where $C(x, t) = mu/(1 + aS + bR)$. We show next that

$$\lim_{t \to \infty} w(x, t) = 0 \qquad \text{uniformly in } [0, 1]. \tag{3.8}$$

Let $\eta_0 > 0$ and $\psi = \psi(x) > 0$ denote the principal eigenvalue and principal eigenfunction, respectively, of the following problem

$$d\psi_{xx} + \eta_0 \psi = 0,$$
$$\psi_x(0) = 0, \qquad \psi_x(1) + \gamma\psi(1) = 0.$$

Let $0 < \alpha < \eta_0$, $w(x, t) = \psi(x)\, \omega(x, t)\, e^{-\alpha t}$. Then

$$d\omega_{xx} + 2d\frac{\psi_x}{\psi}\omega_x - \omega_t + (\alpha - \eta_0 - C(x, t))\, \omega = 0,$$
$$\omega_x(0, t) = 0, \qquad \omega_x(1, t) = 0,$$
$$\omega(x, 0) = \omega_0(x) \equiv \frac{w_0(x)}{\psi(x)}.$$

It follows from the Maximum Principle that $|\omega(x, t)| \leqslant K'$ for some constant $K' > 0$. This leads to $\max_{0 \leqslant x \leqslant 1} |w(x, t)| \leqslant Ke^{-\alpha t}$, which yields (3.8).

From the above definition of φ and w, we obtain

$$S = \varphi + \frac{c}{1+c} w - \frac{1}{1+c} u, \qquad R = \varphi - \frac{1}{1+c} w - \frac{1}{1+c} u. \tag{3.9}$$

Putting (3.9) into the equation of u in (1.2), we obtain

$$u_t = du_{xx} + m(1+c)\, u \frac{\varphi - \dfrac{u}{1+c}}{\left(1 + \dfrac{ac-b}{1+c} w\right) + (a+b)\left(\varphi - \dfrac{u}{1+c}\right)}, \tag{3.10}$$
$$u_x(0, t) = 0, \qquad u_x(1, t) + \gamma u(1, t) = 0.$$

From (3.7)(3.8), for any $\varepsilon > 0$, there exists $T > 0$ such that $|w| < \varepsilon$, $z - \varepsilon z < \varphi < z + \varepsilon$ for $x \in [0, 1]$, $t \geqslant T$. Hence

$$u_1(x, t) \leqslant \frac{u(x, t)}{1+c} \leqslant u_2(x, t) \qquad \text{for} \quad x \in [0, 1], \quad t \geqslant T,$$

where $u_i(x,t)$, $i=1,2$, satisfies

$$u_{1t}=du_{1xx}+m(1+c)\,u_1\,\frac{z-\varepsilon z-u_1}{\left(1+\frac{|ac-b|}{1+c}\,\varepsilon\right)+(a+b)(z-\varepsilon z-u_1)},$$

$$0<x<1,\quad t>T,$$

$$u_{1x}(0,t)=0,\qquad u_{1x}(1,t)+\gamma u_1(1,t)=0,\qquad t>T, \tag{3.11}$$

$$u_1(x,T)=\min\left(\frac{u(x,T)}{1+c},(1-\varepsilon)\,z\right),\qquad 0<x<1;$$

$$u_{2t}=du_{2xx}+m(1+c)\,u_2\,\frac{z+\varepsilon-u_2}{\left(1-\frac{|ac-b|}{1+c}\,\varepsilon\right)+(a+b)(z+\varepsilon-u_2)},$$

$$0<x<1,\quad t>T,$$

$$u_{2x}(0,t)=0,\qquad u_{2x}(1,t)+\gamma u_2(1,t)=0,\qquad t>T, \tag{3.12}$$

$$u_2(x,T)=\frac{u(x,T)}{1+c},\qquad 0<x<1.$$

If $m<m_0$, then $\lambda_0>(1+c)\,m$. Thus, for sufficiently small ε, there exists the principal eigenvalue λ_ε of the following problem such that $\lambda_\varepsilon>(1+c)\,m$.

$$d\phi^\varepsilon_{xx}+\lambda_\varepsilon F(z,z)\,\phi^\varepsilon=0,$$

$$\phi^\varepsilon_x(0)=0,\qquad \phi^\varepsilon_x(1)+\gamma\phi^\varepsilon(1)=0,$$

where $F(z,\varepsilon)=(z+\varepsilon)/((1-(|ac-b|/1+c)\,\varepsilon)+(a+b)(z+\varepsilon))$, $\phi^\varepsilon>0$ on $[0,1]$ is the corresponding principal eigenfunction. Consider the function $U(x,t)=C\phi^\varepsilon(x)\,e^{\delta((1+c)\,m-\lambda_\varepsilon)(t-T)}$. For large C and small δ we have $0\leqslant u_2(x,t)\leqslant U(x,t)$ for $t\geqslant T$, which implies $\lim_{t\to\infty}u(x,t)=0$ if $m<m_0$. From (3.9) we have $\lim_{t\to\infty}S(x,t)=z$, $\lim_{t\to\infty}R(x,t)=z$.

If $m>m_0$, similarly to the proof of Theorem 2.5 we can prove

$$\lim_{t\to\infty}u_i(x,t)=u_i^\varepsilon(x),\qquad \lim_{\varepsilon\to 0}u_i^\varepsilon(x)=\hat{s}\qquad \text{uniformly for}\quad x\in[0,1],$$

where $u_i^\varepsilon(x)$, $i=1,2$, is the unique positive steady-state solution of (3.11)(3.12) respectively. This leads to $\lim_{t\to\infty}u(x,t)=(1+c)\,\hat{s}$, which gives $\lim_{t\to\infty}S(x,t)=z-\hat{s}$, $\lim_{t\to\infty}R(x,t)=z-\hat{s}$.

3.2. *The Positive Solution for General* (m, n)

In this subsection, we deduce the existence and nonexistence of a positive solution of (3.3)(3.4) in the general case of (m, n). First, we give a basic estimate for (s, r).

LEMMA 3.4. *If* $m \geqslant n$, *then the solution* (s, r) *of* (3.3)(3.4) *satisfies* $r \leqslant s \leqslant m/nr$ *for* $x \in [0, 1]$.

Proof. Let $w = s - r$. Then

$$dw_{xx} - C(x)\, w \leqslant 0, \quad 0 < x < 1; \qquad w_x(0) = 0, \qquad w_x(1) + \gamma w(1) = 0,$$

where $C(x) = n(s + cr)/(1 + a(z - s) + b(z - r)) \geqslant 0$. By the Maximum Principle we have $w \geqslant 0$. Thus, $s \geqslant r$. Next, let $\omega = ns - mr$. Then

$$\begin{aligned} d\omega_{xx} &= mn(s + cr)(g(z - s, z - r) - f(z - s, z - r)) \\ &= \frac{mn(s + cr)}{1 + a(z - s) + b(z - r)}\,(s - r) \geqslant 0, \end{aligned}$$

$$\omega_x(0) = 0, \qquad \omega_x(1) + \gamma\omega(1) = 0.$$

It follows that $\omega \leqslant 0$, i.e., $s \leqslant \frac{m}{n} r$.

Remark 2. Similarly, if $m \leqslant n$, then we have $s \leqslant r \leqslant \frac{n}{m} s$ for $x \in [0, 1]$.

Our following result shows that a positive solution of (3.3) cannot exist if both m and n are too small.

THEOREM 3.5. *Suppose* $\max(m, n) \leqslant \lambda_0/(1 + c)$. *Then* $(s, r) = (0, 0)$ *is the unique nonnegative solution of* (3.3)(3.4).

Proof. If $n \leqslant m \leqslant \lambda_0/(1 + c)$, and (s, r) is a nontrivial nonnegative solution of (3.3)(3.4), then we know from the Maximum Principle that $s > 0$, $r > 0$. Multiplying the first equation in (3.3) by s, integrating over $(0, 1)$, and using Green's formula we find

$$\begin{aligned} d \int_0^1 s_x^2\, dx + d\gamma s^2(1) &= m \int_0^1 (s + cr)\, sf(z - s, z - r)\, dx \\ &< m(1 + c) \int_0^1 s^2 f(z, z)\, dx. \end{aligned}$$

By the variational property of the principal eigenvalue it follows that

$$d \int_0^1 s_x^2\, dx + d\gamma s^2(1) \geqslant \lambda_0 \int_0^1 s^2 f(z, z)\, dx.$$

Hence $(\lambda_0 - m(1+c)) \int_0^1 s^2 f(z, z)\, dx < 0$, which leads to $s=0$, a contradiction. A similar result holds if $m \leqslant n \leqslant \lambda_0/(1+c)$. This completes the proof.

Remark 3. Suppose $\max(m, n) \leqslant \lambda_0/(1+c)$. Then the washout solution $(z, z, 0)$ is the unique nontrivial nonnegative solution of (3.1)(3.2).

If both m and n are greater than some critical value, in our next result we prove that a positive solution actually exists.

THEOREM 3.6. *Suppose* $\min(m, n) > \lambda_0/(1+c)$. *Then there exists a positive solution of* (3.3)(3.4).

Proof. It is easy to check that (3.3)(3.4) is a quasi-monotone increasing system. Thus it suffices to construct the suitable upper and lower solutions. Let $(\bar{s}, \bar{r}) = (z, z)$ and $(\underline{s}, \underline{r}) = (\delta\phi, \delta\phi)$, where ϕ is the principal eigenfunction defined by (3.6) and $\delta > 0$ is small enough. Obviously, $(\bar{s}, \bar{r})$ is the upper solution of (3.3)(3.4). $(\underline{s}, \underline{r})$ satisfies

$$\begin{aligned} &d\underline{s}_{xx} + m(\underline{s} + c\underline{r})\, f(z - \underline{s}, z - \underline{r}) \\ &\quad = \underline{s}[(m(1+c) - \lambda_0)\, f(z, z) - m(1+c)(f(z, z) - f(z - \delta\phi, z - \delta\phi))] \\ &\quad \geqslant \underline{s} \left[\frac{(m(1+c) - \lambda_0)}{\gamma + a + b} - \frac{m(1+c)\, \delta\phi}{(1 + (a+b)(z - \theta\delta\phi))^2} \right] \qquad (0 < \theta < 1). \end{aligned}$$

As long as δ is sufficiently small, we have

$$d\underline{s}_{xx} + m(\underline{s} + c\underline{r})\, f(z - \underline{s}, z - \underline{r}) > 0.$$

By the same reasoning we obtain

$$d\underline{r}_{xx} + n(\underline{s} + c\underline{r})\, g(z - \underline{s}, z - \underline{r}) > 0.$$

Thus, for small δ, the pair $(\bar{s}, \bar{r})$ and $(\underline{s}, \underline{r})$ are the ordered upper and lower solutions of (3.3)(3.4). It follows from the existence-comparison theorem [25] for elliptic systems that the minimal and maximal solution (s_i, r_i) $(i = 1, 2)$ to (3.3)(3.4) exist and satisfy the relation $(\delta\phi, \delta\phi) \leqslant (s_1, r_1) \leqslant (s_2, r_2) \leqslant (z, z)$.

If the condition of Theorem 3.6 does not hold, but either m or n is a little larger, we also have

THEOREM 3.7. *Suppose that either* $m > \lambda_0$, $n \leqslant \lambda_0/(1+c)$ *or* $n > \lambda_0/c$, $m \leqslant \lambda_0/(1+c)$. *Then the conclusion of Theorem* 3.6 *holds.*

Proof. We focus on the former case, since the other case can be done similarly. As above, let $(\bar{s}, \bar{r}) = (z, z)$ and $(\underline{s}, \underline{r}) = (\delta\phi, 0)$. Then

$$d\underline{s}_{xx} + m(\underline{s} + c\underline{r})\, f(z - \underline{s}, z - \underline{r})$$
$$= \underline{s}[(m - \lambda_0)\, f(z, z) - m(f(z, z) - f(z - \delta\phi, z))].$$

For small $\delta > 0$, we note that $(\bar{s}, \bar{r})$ and $(\underline{s}, \underline{r})$ are the ordered upper and lower solution of (3.3)(3.4). Hence there exists solution (s, r) of (3.3)(3.4) such that $(\delta\phi, 0) \leqslant (s, r) \leqslant (z, z)$. So $s > 0$. We claim $r \not\equiv 0$, otherwise by Lemma 3.4 $s = 0$, a contradiction. From the Maximum Principle it follows that $r > 0$. This completes the proof.

If $bm - acn \geqslant 0$, it is considered in Ref. [10] that the resource S is superior to resource R in the sense that the maximal growth rate is larger.

THEOREM 3.8. *Suppose* $\frac{m}{n} \geqslant \max(1, \frac{ac}{b})$, *and* $m + cn \leqslant \lambda_0$. *Then* $(0, 0)$ *is the unique nonnegative solution of* (3.3)(3.4).

Proof. If (s, r) is the nontrivial nonnegative solution of (3.3)(3.4), then we know as before that $s > 0$, $r > 0$. From (3.3) it is easy to see that

$$d(s + cr)_{xx} + m(s + cr)\, f(z - s, z - r) + cn(s + cr)\, g(z - s, z - r) = 0.$$

Multiplying the equation by $s + cr$, integrating over $(0, 1)$, and using Green's formula we find

$$d \int_0^1 (s + cr)_x^2\, dx + d\gamma(s(1) + cr(1))^2$$
$$= \int_0^1 (s + cr)^2\, [mf(z - s, z - r) + cng(z - s, z - r)]\, dx$$
$$< (m + cn) \int_0^1 (s + cr)^2\, f(z, z)\, dx.$$

In the above argument we have used that $mf(z - s, z - r) + cng(z - s, z - r) < (m + cn)\, f(z, z)$, which is easily proved from $bm - acn \geqslant 0$ and Lemma 3.4. From the variational property we know

$$d \int_0^1 (s + cr)_x^2\, dx + d\gamma(s(1) + cr(1))^2 \geqslant \lambda_0 \int_0^1 (s + cr)^2\, f(z, z)\, dx.$$

By combination of the two inequalities we can complete the proof.

Remark 4. A similar result holds in the other case: $\frac{m}{n} \leqslant \min(1, \frac{ac}{b})$ and $m + cn \leqslant \lambda_0$.

In the following, our goal is to examine the stability of the washout solution. The other reason for doing this is to find a condition so that bifurcation theory can be used to obtain a positive solution.

THEOREM 3.9. *The washout solution* $(z, z, 0)$ *of* (1.2) *is linearly stable if* $m + cn < \lambda_0$ *and unstable if* $m + cn > \lambda_0$.

Proof. The linearization of (1.2)(1.3) with respect to the washout solution $(z, z, 0)$ leads to

$$\begin{aligned} d\psi_{1xx} + mf(z, z)\,\psi_3 &= \lambda\psi_1, \\ d\psi_{2xx} + ng(z, z)\,\psi_3 &= \lambda\psi_2, \\ d\psi_{3xx} + (mf(z, z) + cng(z, z))\,\psi_3 &= \lambda\psi_3, \\ \psi_{ix}(0) = 0, \qquad \psi_{ix}(1) + \gamma\psi_i(1) &= 0, \qquad i = 1, 2, 3. \end{aligned} \tag{3.13}$$

Let η_0, η_1 be the principal eigenvalue of the following operator with the usual boundary conditions respectively,

$$L_0 = d\frac{d^2}{dx^2}, \qquad L_1 = d\frac{d^2}{dx^2} + (mf(z, z) + cng(z, z)).$$

Then it is easy to check that $\eta_0 < 0$, $\eta_1 > \eta_0$. If $\psi_3 \equiv 0$, then $\lambda = \eta_0$ is an eigenvalue of (3.13); if $\psi_3 \not\equiv 0$, then $\lambda = \eta_1$ is the largest eigenvalue of the operator L_1, and the corresponding eigenfunction is $\psi_3 > 0$. From $\eta_1 - \eta_0 > 0$, it follows that

$$\psi_1 = (-L_0 + \eta_1)^{-1}\,(mf(z, z)\,\psi_3) > 0, \quad \psi_2 = (-L_0 + \eta_1)^{-1}\,(ng(z, z)\,\psi_3) > 0,$$

where $(-L_0 + \eta_1)^{-1}$ is the inverse operator of $(-L_0 + \eta_1)$. Thus we find that η_1 is the largest eigenvalue of (3.13).

Noting that $f(z, z) = g(z, z)$, and using the comparison property of the principal eigenvalue, we know from (3.6) that $\eta_1 < 0$ if $m + cn < \lambda_0$; and $\eta_1 > 0$ if $m + cn > \lambda_0$. This completes the proof.

Next, for fixed $n \leqslant \lambda_0/(1 + c)$, we treat m as a bifurcation parameter to obtain the global bifurcation which corresponds to the positive solution of (3.3)(3.4).

At first, we rewrite (3.3)(3.4) as

$$\begin{aligned} ds_{xx} + m(s + cr)\,f(z, z) + F_1(s, r) &= 0, \\ dr_{xx} + n(s + cr)\,g(z, z) + F_2(s, r) &= 0, \end{aligned}$$

where

$$F_1(s, r) = m(s + cr)(f(z - s, z - r) - f(z, z)),$$

$$F_2(s, r) = n(s + cr)(g(z - s, z - r) - g(z, z)).$$

Let K be the inverse operator of $-d(d^2/dx^2)$. Then

$$s - mK((s + cr)\, f(z, z)) - KF_1(s, r) = 0,$$

$$r - nK((s + cr)\, g(z, z)) - KF_2(s, r) = 0.$$

Let $T(m; s, r) = (mK((s + cr)\, f(z, z)) + KF_1(s, r),\ \ nK((s + cr)\, g(z, z)) + KF_2(s, r))$, and $G(m; s, r) = (s, r) - T(m; s, r)$. Then the zeros of $G(m; s, r)$ are the solutions of (3.3)(3.4). Set $C_B^1[0, 1] = \{u(x) \in C^1[0, 1] : u_x(0) = 0, u_x(1) + \gamma u(1) = 0\}$, endowed with the usual norm $\|\cdot\|$, and $X = C_B^1[0, 1] \times C_B^1[0, 1]$.

THEOREM 3.10. *Suppose* $n \leqslant \lambda_0/(1 + c)$. *Then* $(m_0; 0, 0)$ *is a bifurcation point of* $G(m; s, r) = 0$, *and in the neighbourhood of* $(m_0; 0, 0)$, *part of the bifurcation branch corresponds to the positive solution of* (3.3)(3.4), *where* $m_0 = \lambda_0 - cn$.

Proof. The Frechet derivative of $G(m; s, r)$ with respect to (s, r) at $(0, 0)$ is denoted by $L(m; 0, 0) = D_{(s, r)} G(m; 0, 0)$. Straightforward computation gives

$$L(m_0; 0, 0) \cdot (w, \chi) = (w - m_0 K((w + c\chi)\, f(z, z)), \chi - nK((s + cr)\, g(z, z))).$$

Then $L(m_0; 0, 0) \cdot (w, \chi) = 0$ leads to

$$dw_{xx} + m_0(w + c\chi)\, f(z, z) = 0,$$

$$d\chi_{xx} + n(w + c\chi)\, g(z, z) = 0,$$

$$w_x(0) = 0, \qquad \chi_x(0) = 0,$$

$$w_x(1) + \gamma w(1) = 0, \qquad \chi_x(1) + \gamma \chi(1) = 0.$$

Noting that $f(z, z) = g(z, z)$ and $m_0 + cn = \lambda_0$, we can take $w + c\chi = \phi$. Putting this into the above equation we find

$$-dw_{xx} = m_0\, f(z, z)\, \phi, \qquad -d\chi_{xx} = ng(z, z)\, \phi.$$

It is easy to show that there exists a unique positive solution (w_1, χ_1) of the above problem. Moreover, $w_1 \geqslant \chi_1$ and $w_1 + c\chi_1 = \phi$. Hence the null space of $L(m_0; 0, 0)$, $N(L(m_0; 0, 0)) = \text{spans}\{(w_1, \chi_1)\}$.

Suppose that $(h_1, h_2) \in R(L(m_0; 0, 0))$, the range of the operator $L(m_0; 0, 0)$. Then there exists $(\Phi, \Psi) \in X$ such that

$$\Phi - m_0 K((\Phi + c\Psi) f(z, z)) = h_1,$$

$$\Psi - nK((\Phi + c\Psi) g(z, z)) = h_2,$$

which gives

$$d\Phi_{xx} + m_0(\Phi + c\Psi) f(z, z) = dh_{1xx},$$

$$d\Psi_{xx} + n(\Phi + c\Psi) g(z, z) = dh_{2xx},$$

$$\Phi_x(0) = \Psi_x(0) = 0,$$

$$\Phi_x(1) + \gamma\Phi(1) = 0, \qquad \Psi_x(1) + \gamma\Psi(1) = 0.$$

Thus we find

$$d(\Phi + c\Psi)_{xx} + \lambda_0(\Phi + c\Psi) f(z, z) = d(h_1 + ch_2)_{xx}.$$

It follows from the Fredholm alternative that

$$0 = \int_0^1 d\phi(h_1 + ch_2)_{xx}\, dx = -\int_0^1 \lambda_0 f(z, z)\, \phi(h_1 + ch_2)\, dx,$$

which implies $R(L(m_0; 0, 0)) = \{(h_1, h_2) \in X : \int_0^1 f(z, z)\, \phi(h_1 + ch_2)\, dx = 0\}$ and codim $R(L(m_0; 0, 0)) = 1$.

Let $L_1 \cdot (w, \chi) = D_m D_{(s, r)} G(m_0; 0, 0) \cdot (w, \chi) = (-K((w + c\chi) f(z, z)), 0)$ be the Frechet derivative of second order. Then it is easy to see that $L_1 \cdot (w_1, \chi_1) \notin R(L(m_0; 0, 0))$.

By application of Theorem 1.7 [26] bifurcating from a simple eigenvalue, there exists a $\tau_0 > 0$ and C^1 function $(m(\tau); s(\tau), r(\tau))$: $(-\tau, \tau) \to R \times X$ such that $m(0) = m_0$, $w(0) = \chi(0) = 0$ and $(m(\tau); s(\tau), r(\tau)) = (m(\tau); \tau(w_1 + w(\tau)), \tau(\chi_1 + \chi(\tau)))(|\tau| < \tau_0)$, which is the solution of (3.3)(3.4). If we take $0 < \tau < \tau_0$, this bifurcation branch is just the positive solution of (3.3)(3.4).

Suppose that the hypothesis of Theorem 3.10 holds, and $bm_0 - acn \geqslant 0$. Then we can show that the bifurcating positive solution defined in Theorem 3.10 is to the right in the neighbourhood of $(m_0; 0, 0)$.

THEOREM 3.11. *Suppose* $bm_0 - acn \geqslant 0$. *Then under the condition of Theorem* 3.10, *the bifurcation of a positive solution is to the right.*

Proof. Substitute $(m(\tau); \tau(w_1 + w(\tau)), \tau(\chi_1 + \chi(\tau)))$ into (3.3), divide by τ, differentiate with respect to τ, and set $\tau = 0$. Then we get

$$\begin{aligned}
&dw'_{xx}(0) + m'(0)(w_1 + c\chi_1)\, f(z, z) + m_0(w'(0) + c\chi'(0))\, f(z, z) \\
&\qquad + m_0(w_1 + c\chi_1)(-f'_1(z, z)\, w_1 - f'_2(z, z)\, \chi_1) = 0, \\
&d\chi'_{xx}(0) + n(w'(0) + c\chi'(0))\, g(z, z) + n(w_1 + c\chi_1)(-g'_1(z, z)\, w_1 \\
&\qquad - g'_2(z, z)\, \chi_1) = 0, \\
&\qquad\qquad w_x(0) = 0, \qquad \chi_x(0) = 0, \\
&w_x(1) + \gamma w(1) = 0, \qquad \chi_x(1) + \gamma\chi(1) = 0,
\end{aligned}$$

where $w'(0), \chi'(0)$ represent the derivative of w and χ with respect to τ at $\tau = 0$, and f'_i, g'_i represent the derivative of f and g with respect to the ith variable. Multiplying the second equation of $\chi'(0)$ by c, adding to the first equation of $w'(0)$, integrating over $(0, 1)$, and noting $w_1 + c\chi_1 = \phi$, we have

$$\begin{aligned}
m'(0) \int_0^1 \phi^2 f(z, z)\, dx = \int_0^1 \phi^2 [m_0(f'_1(z, z)\, w_1 + f'_2(z, z)\, \chi_1) \\
+ cn(g'_1(z, z)\, w_1 + g'_2(z, z)\, \chi_1)]\, dx.
\end{aligned}$$

In the above argument, we have used

$$\begin{aligned}
&\int_0^1 [d(w'(0) + c\chi'(0))_{xx}\, \phi + \lambda_0(w'(0) + c\chi'(0))\, f(z, z)\, \phi]\, dx \\
&\qquad = \int_0^1 (w'(0) + c\chi'(0))[d\phi_{xx} + \lambda_0 f(z, z)\, \phi]\, dx = 0.
\end{aligned}$$

Noting $\int_0^1 \phi^2 f(z, z)\, dx = 1$, it is easy to see that

$$\begin{aligned}
m'(0) = \int_0^1 \frac{\phi^2}{(1 + (a + b)\, z)^2} [(m_0(1 + bz) - acnz)\, w_1 \\
+ (cn(1 + az) - bm_0 z)\, \chi_1]\, dx.
\end{aligned}$$

Since $bm_0 - acn \geqslant 0$, and $w_1 \geqslant \chi_1$, we have $m'(0) \geqslant \int_0^1 (\lambda_0 \phi^2 \chi_1)/(1 + (a + b)\, z)^2\, dx > 0$. Hence for $0 < \tau \ll 1$, it is easy to show that $m(\tau) > m_0$, which implies $m(\tau) + cn > \lambda_0$ for $0 < \tau \ll 1$.

Remark 5. (i) Suppose that $\frac{m_0}{n} \geqslant \max(1, \frac{ca}{b})$. Then by comparison of Theorem 3.8 and Theorem 3.10–3.11, it follows that (3.3) has only the trivial solution $(0, 0)$ if $m + cn \leqslant \lambda_0$; and the unique positive solution if $m(\tau) + cn > 1$ for $0 < \tau \ll 1$.

(ii) For $m \leqslant \lambda_0/(1+c)$, let $n_0 = (\lambda_0 - m)/c$. A result similar to Theorem 3.10–3.11 holds by treating n as bifurcation parameter at the point $(n_0; 0, 0)$.

We continue to show that the local bifurcation of a positive solution in Theorem 3.10 can be extended to a global bifurcation. We first state the theorem for global bifurcation, that is needed later and can be proved by using exactly the same argument as Ref. [27].

Let $T: R \times X \to X$ be a compact, continuously differentiable operator such that $T(m, 0) = 0$. Suppose T can be written as $T(m, u) = K(m)\, u + R(m, u)$, where $K(m)$ is a linear compact operator and the Frechet derivative of R, $R_u(m, 0) = 0$. Treating m as bifurcation parameter, we investigate the bifurcating solutions of the equation $u = T(m, u)$. If x_0 is an isolated fixed point of T, we define $i(T, x_0)$, the index of T at x_0 as usual. Then we have

THEOREM A. *Let m_0 be such that $I - K(m)$ is invertible if $0 < |m - m_0| < \varepsilon$ for some $\varepsilon > 0$. Suppose $i(T(m, \cdot), 0)$ is constant on $(m_0 - \varepsilon, m_0)$ and $(m_0, m_0 + \varepsilon)$ such that if $m_0 - \varepsilon < m_1 < m_0 < m_2 < m_0 + \varepsilon$, then $i(T(m_1, \cdot), 0) \neq (T(m_2, \cdot), 0)$. Then there exists a continuum C in $(m - u)$ plane of solutions of $u = T(m, u)$ such that one of the following alternatives holds*

(i) *C joins $(m_0, 0)$ to $(\hat{m}, 0)$, where $I - K(\hat{m})$ is not invertible and $\hat{m} \neq m_0$;*

(ii) *C joins $(m_0, 0)$ to ∞ in $R \times X$.*

Let $P = \{(m; s, r) \in R^+ \times X : s > 0,\ r > 0 \text{ on } [0, 1]\}$. Then we have

THEOREM 3.12. *Suppose $n \leqslant \lambda_0/(1+c)$. Then the positive bifurcating solution defined by Theorem 3.10 can be extended to ∞ in P by increasing m.*

Proof. Let $L(m)$ be the Frechet derivative of $T(m; s, r)$ with respect to (s, r) at $(m; 0, 0)$. Then

$$\begin{aligned} L(m) \cdot (w, \chi) &= D_{(w, \chi)} T(m; 0, 0) \\ &= (mK((w + c\chi)\, f(z, z)), nK((w + c\chi)\, g(z, z))). \end{aligned}$$

Suppose that $\lambda \geqslant 1$ is an eigenvalue of $L(m)$ with the corresponding eigenfunction $(w, \chi) \not\equiv 0$. Then

$$\begin{aligned} d\lambda w_{xx} + m(w + c\chi)\, f(z, z) &= 0, \\ d\lambda \chi_{xx} + n(w + c\chi)\, g(z, z) &= 0, \\ w_x(0) = 0, \qquad \chi_x(0) &= 0, \\ w_x(1) + \gamma w(1) = 0, \qquad \chi_x(1) + \gamma\chi(1) &= 0. \end{aligned} \tag{3.14}$$

It is easy to see that

$$d\lambda(w+c\chi)_{xx}+(m+cn)(w+c\chi)\, f(z,z)=0.$$

If $w+c\chi\equiv 0$, then we deduce from (3.14) that $w\equiv 0$, $\chi\equiv 0$, a contradiction. Thus, $w+c\chi\not\equiv 0$, which implies that $m+cn=\mu_i(\lambda)$ for some $i=0, 1, 2, ...$, where $\mu_i(\lambda)$ $(i=0, 1, 2, ...)$ is the eigenvalue of following problem

$$\begin{aligned} d\lambda\psi_{xx}+\mu_i(\lambda)\, f(z,z)\,\psi&=0,\\ \psi_x(0)=0,\qquad \psi_x(1)+\gamma\psi(1)&=0. \end{aligned}\tag{3.15}$$

It is easy to check that $\mu_i(\lambda)$ is increasing with respect to $\lambda\geqslant 1$ and can be ordered as

$$0<\mu_0(\lambda)<\mu_1(\lambda)\leqslant\cdots\qquad\text{and}\quad \mu_0(1)=\lambda_0.$$

Conversely, for any $\lambda\geqslant 1$, if $m+cn$ is one of the eigenvalues $\mu_i(\lambda)$ for some i, then $(w,\chi)\not\equiv 0$ is the corresponding eigenfunction of $L(m)$.

Thus $\lambda\geqslant 1$ is an eigenvalue of $L(m)$, if and only if $m+cn=\mu_i(\lambda)$, for some $i=0, 1, 2, ...$

Suppose $m<m_0$. Then $m+cn<\lambda_0$, which gives $m+cn<\mu_i(\lambda)$ for $i=0$, 1, 2, ... and $\lambda\geqslant 1$. Thus $\lambda=1$ is not an eigenvalue of $L(m)$, and there is no eigenvalue λ which is greater than 1. So $i(T(m;\cdot),0)=1$ in this case.

Suppose $m_0<m<\mu_1(1)-cn$. Then $\lambda_0<m+cn<\mu_1(1)$, which leads to $m+cn<\mu_i(\lambda)$ for $i=1, 2, ...$ and $\lambda\geqslant 1$. Since $\mu_0(1)=\lambda_0$, $\lim_{\lambda\to+\infty}\mu_0(\lambda)=+\infty$, there is a unique $\lambda_1>1$ such that $m+cn=\mu_0(\lambda_1)$. It follows from (3.14) that

$$\begin{aligned} d\lambda_1 w_{xx}+m(w+c\chi)\, f(z,z)&=0,\\ d\lambda_1\chi_{xx}+n(w+c\chi)\, g(z,z)&=0,\\ w_x(0)=0,\qquad \chi_x(0)&=0,\\ w_x(1)+\gamma w(1)=0,\qquad \chi_x(1)+\gamma\chi(1)&=0, \end{aligned}\tag{3.16}$$

which leads to

$$d\lambda_1(w+c\chi)_{xx}+\mu_0(\lambda_1)(w+c\chi)\, f(z,z)=0.$$

Thus $w+c\chi=\Phi_0$, where Φ_0 is the principal eigenfunction of (3.15) corresponding to $\mu_0(\lambda_1)$. From (3.16), we obtain

$$N(\lambda_1 I-L(m))=\operatorname{span}\{(\hat{w},\hat{\chi})\}\qquad\text{and}\qquad \dim N(\lambda_1 I-L(m))=1,$$

where $\hat{w}+c\hat{\chi}=\Phi_0$, and $(\hat{w}, \hat{\chi})$ is the unique positive solution of the following problem

$$-d\lambda_1\hat{w}_{xx}=m\Phi_0\, f(z,z),$$

$$-d\lambda_1\hat{\chi}_{xx}=n\Phi_0\, g(z,z)$$

with the usual boundary conditions.

Next, we are prepared to show that $N(\lambda_1 I-L(m))\cap R(\lambda_1 I-L(m))=0$. If not, without loss of generality we may assume that $(\hat{w}, \hat{\chi})\in R(\lambda_1 I-L(m))$. Then there exists $(w, \chi)\in X$ such that

$$d\lambda_1 w_{xx}+m(w+c\chi)\, f(z,z)=d\hat{w}_{xx},$$

$$d\lambda_1\chi_{xx}+n(w+c\chi)\, g(z,z)=d\hat{\chi}_{xx}$$

with the usual boundary conditions.

It follows that

$$d\lambda_1(w+c\chi)_{xx}+\mu_0(\lambda_1)(w+c\chi)\, f(z,z)=d(\hat{w}+c\hat{\chi})_{xx}.$$

Multiplying by Φ_0, integrating over $(0,1)$, and using Green's formula we get

$$\begin{aligned}\int_0^1 d(\hat{w}+c\hat{\chi})_{xx}\Phi_0\,dx&=\int_0^1 (d\lambda_1(w+c\chi)_{xx}+\mu_0(\lambda_1)(w+c\chi)\, f(z,z))\,\Phi_0\,dx\\&=\int_0^1 (d\lambda_1\Phi_{0xx}+\mu_0(\lambda_1)\,\Phi_0\, f(z,z))(w+c\chi)\,dx=0.\end{aligned}$$

Noting $\hat{w}+c\hat{\chi}=\Phi_0$, we find that the lefthand side of the above identity equals $\int_0^1 d\Phi_{0xx}\Phi_0\,dx=-\mu_0(\lambda_1)/\lambda_1\int_0^1\Phi_0^2 f(z,z)\,dx<0$, which leads to a contradiction. So we know that $\lambda_1>1$ is an eigenvalue of $L(m)$, whose multiplicity is one. This gives $i(T(m;\cdot),0)=-1$ in the case of $m_0<m<\mu_1(1)-cn$.

Theorem A can be applied to obtain the existence of a continuum C_1 of solutions of $(s,r)=T(m;s,r)$ in $R^+\times X$ bifurcating from $(m_0;0,0)$, which, in the neighbourhood of $(m_0;0,0)$, coincides with the bifurcating solution given in Theorem 3.10. Let $C=C_1-\{(m(\tau);s(\tau),r(\tau)): -\delta<\tau<0\}$. Then $C-\{(m_0;0,0)\}\subset P$ in the small neighbourhood of $(m_0;0,0)$.

Now we want to claim that $C-\{(m_0;0,0)\}\subset P$. If not, there exists $(\hat{m};\hat{s},\hat{r})\in\{C-(m_0;0,0)\}\cap\partial P$ which is the limit of a sequence

$$\{(m_{n'};s_{n'},r_{n'})\}\subset C\cap P,\quad s_{n'}>0,\quad r_{n'}>0\quad\text{on }[0,1],\qquad n'=1,2,...,$$

where ∂P denotes the boundary of P. Owing to $(\hat{m}; \hat{s}, \hat{r}) \in \partial P$, there exists $x_0 \in [0, 1]$ such that either $\hat{s}(x_0) = 0$ or $\hat{r}(x_0) = 0$. Since $(\hat{m}; \hat{s}, \hat{r})$ satisfies

$$d\hat{s}_{xx} + \hat{m}(\hat{s} + c\hat{r})\, f(z - \hat{s}, z - \hat{r}) = 0,$$

$$d\hat{r}_{xx} + n(\hat{s} + c\hat{r})\, g(z - \hat{s}, z - \hat{r}) = 0$$

with the usual boundary conditions, we can proceed as before to prove that either $\hat{s} \equiv 0$ or $\hat{r} \equiv 0$. By using Lemma 3.4 and Remark 2, this leads to $(\hat{s}, \hat{r}) \equiv (0, 0)$ in either case. Therefore, $m_{n'} \to \hat{m}$, $(s_{n'}, r_{n'}) \to (0, 0)$ in X as $n' \to \infty$. Since $(m_{n'}; s_{n'}, r_{n'})$ satisfies

$$ds_{n'xx} + m_{n'}(s_{n'} + cr_{n'})\, f(z - s_{n'}, z - r_{n'}) = 0,$$

$$dr_{n'xx} + n(s_{n'} + cr_{n'})\, g(z - s_{n'}, z - r_{n'}) = 0$$

with the usual boundary conditions, we obtain as above

$$d(s_{n'} + cr_{n'})_{xx} + m_{n'}(s_{n'} + cr_{n'})\, f(z - s_{n'}, z - r_{n'})$$
$$+ cn(s_{n'} + cr_{n'})\, g(z - s_{n'}, z - r_{n'}) = 0.$$

Set $V_{n'} = (s_{n'} + cr_{n'})/\|s_{n'} + cr_{n'}\|$. Then

$$dV_{n'xx} + m_{n'} V_{n'}\, f(z - s_{n'}, z - r_{n'}) + cnV_{n'}\, g(z - s_{n'}, z - r_{n'}) = 0,$$
$$V_{n'x}(0) = 0, \qquad V_{n'x}(1) + \gamma V_{n'}(1) = 0.$$

By the L^p estimate for the elliptic equation and the Sobolev Embedding Theorem, passing to a subsequence if necessary, there exists $V \geqslant 0$, $\not\equiv 0$ such that $V_{n'} \to V$ in C^1 as $n' \to \infty$. Hence V satisfies the problem weakly

$$dV_{xx} + (\hat{m} + cn)\, Vf(z, z) = 0,$$
$$V_x(0) = 0, \qquad V_x(1) + \gamma V(1) = 0.$$

Regularity of the elliptic equation leads to $V \in C^2$. Moreover, by the Maximum Principle we deduce that $V > 0$ on $[0, 1]$. Hence $\hat{m} = \lambda_0 - cn = m_0$, contradicting the definition of $\hat{m}$.

From Theorem A and the reflection method used in Ref. [27], it follows that the continuum $C - \{(m_0; 0, 0)\}$ must satisfy either of the alternatives in Theorem A or contain symmetric points of the form $(m; s, r)$ and $(m; -s, -r)$. By the argument above, we know that the only possibility is that C extends to ∞ in P. If $\{m\colon (m; s, r) \in C\}$ is bounded, noting $0 \leqslant s, r < z$ and using the L^p estimate and the Sobolev Embedding Theorem, we find $\|(s, r)\|$ is bounded in X, a contradiction. Therefore the only way for C to extend to ∞ in P is to let m increase to ∞. This completes the proof.

3.3. *The Longtime Behavior of the Limiting System*

As noted in Refs. [15, 16], for the system (1.2), there exists $\alpha > 0$ such that $|S(x,t) + cR(x,t) + u(x,t) - (1+c)z| = O(e^{-\alpha t})$ as $t \to \infty$. This allows us to first study the longtime behavior of (1.2)–(1.4) by restricting our attention to the invariant exponentially attracting set given by $S + cR + u = (1+c)z$. Just as in Refs. [15, 16, 28], the relevant limiting system is as follows

$$\begin{aligned} S_t &= dS_{xx} - m((1+c)z - S - cR) f(S,R), \\ R_t &= dR_{xx} - n((1+c)z - S - cR) g(S,R) \end{aligned} \tag{3.17}$$

with boundary conditions

$$\begin{aligned} S_x(0,t) &= -1, & R_x(0,t) &= -1, \\ S_x(1,t) + \gamma S(1,t) &= 0, & R_x(1,t) + \gamma R(1,t) &= 0 \end{aligned} \tag{3.18}$$

and initial conditions

$$S(x,0) = S_0(x), \qquad R(x,0) = R_0(x), \tag{3.19}$$

where $S_0(x), R_0(x) \in C^+[0,1]$, and $S_0(x) + cR_0(x) \leqslant (1+c)z, \not\equiv (1+c)z$.

Because (S, R) is of inhomogeneous boundary conditions, it needs to be dealt with more delicately.

The local existence of (3.17)–(3.19) is standard as in Ref. [24]. It follows from the Maximum Principle that $S(x,t) > 0$, $R(x,t) > 0$. Let $W = (1+c)z - S - cR$. Then we have

$$\begin{gathered} W_t = dW_{xx} + (mf(S,R) + cng(S,R))\, W, \\ W_x(0,t) = 0, \qquad W_x(1,t) + \gamma W(1,t) = 0, \\ W(x,0) = W_0(x) \equiv (1+c)z - S_0 - cR_0 \geqslant 0, \not\equiv 0. \end{gathered} \tag{3.20}$$

Thus $W(x,t) > 0$, i.e., $S(x,t) + cR(x,t) < (1+c)z$. This implies the global existence of (3.17)–(3.19).

Let $\hat{\lambda}_0$ be the principal eigenvalue of

$$\begin{gathered} d\hat{\phi}_{xx} + \hat{\lambda}_0 F(z)\, \hat{\phi} = 0, \\ \hat{\phi}_x(0) = 0, \qquad \hat{\phi}_x + \gamma \hat{\phi}(1) = 0, \end{gathered}$$

where $F(z) = z/(1/(1+c) + \max(a, b/c)\, z)$. Since $(1+c) f(z,z) \geqslant F(z) > \min(1,c) f(z,z)$, it is easily verified that $\lambda_0/(1+c) \leqslant \hat{\lambda}_0 < \lambda_0 \max(1, 1/c)$.

LEMMA 3.13. *Suppose* $\min(m, n) > \hat{\lambda}_0$. *Then there exist constants* $\alpha_0 > 0$, $t_0 > 0$ *such that* $(1+c)\,z - S(x, t) - cR(x, t) \geqslant \alpha_0$ *for* $x \in [0, 1]$, $t \geqslant t_0$.

Proof. Denote $W = (1+c)\,z - S - cR$. Then

$$mf(S, R) + cng(S, R) \geqslant \frac{\min(m, n)(S + cR)}{1 + \max\left(a, \dfrac{b}{c}\right)(S + cR)}$$

$$= \min(m, n)\,\frac{z - \dfrac{W}{1+c}}{\dfrac{1}{1+c} + \max\left(a, \dfrac{b}{c}\right)\left(z - \dfrac{W}{1+c}\right)}$$

$$\triangleq \min(m, n)\,F\left(z - \frac{W}{1+c}\right).$$

It follows from the Comparison Theorem and (3.20) that $\frac{W}{1+c} \geqslant \omega$, where $\omega(x, t)$ is the solution of

$$\omega_t = d\omega_{xx} + \min(m, n)\,\omega F(z - \omega),$$

$$\omega_x(0, t) = 0, \qquad \omega_x(1, t) + \gamma\omega(1, t) = 0,$$

$$\omega(x, 0) = \frac{W_0(x)}{1+c}.$$

As before, it can be proved that there exists a unique corresponding positive steady-state solution $\omega^*(x)$ as long as $\min(m, n) > \hat{\lambda}_0$. Moreover, $\lim_{t \to \infty} \omega(x, t) = \omega^*(x)$ uniformly for $x \in [0, 1]$. Hence there exist constants $\alpha_0 > 0$, $t_0 > 0$ such that $\omega(x, t) \geqslant \alpha_0/(1+c)$ for $x \in [0, 1]$, $t \geqslant t_0$, which implies $(1+c)\,z - S - cR \geqslant \alpha_0$ for $x \in [0, 1]$, $t \geqslant t_0$.

LEMMA 3.14. *There exist constants* $\alpha_1 > 0$, $t_1 > 0$ *such that the solution* (S, R) *of* (3.17)–(3.19) *satisfies* $S(x, t) \geqslant \alpha_1$, $R(x, t) \geqslant \alpha_1$ *for* $x \in [0, 1]$, $t \geqslant t_1$.

Proof. Set $c_1 = \max(2, 1+c)$. By (3.7) we find

$$S_t \geqslant dS_{xx} - m((1+c)\,z - S)\,S \geqslant dS_{xx} - m(c_1 z - S)\,S.$$

From the Comparison Theorem it follows that $S(x, t) \geqslant \beta(x, t)$ for $x \in [0, 1]$, $t > 0$, where $\beta(x, t)$ satisfies

$$\begin{aligned} &\beta_t = d\beta_{xx} - m(c_1 z - \beta)\,\beta, \\ &\beta_x(0, t) = -1, \qquad \beta_x(1, t) + \gamma\beta(1, t) = 0, \\ &\beta(x, 0) = \beta_0(x) \equiv S_0(x). \end{aligned} \tag{3.21}$$

Now consider the corresponding steady-state equation

$$d\beta_{xx} - m(c_1 z - \beta)\,\beta = 0; \qquad \beta_x(0) = -1, \qquad \beta_x(1) + \gamma\beta(1) = 0. \tag{3.22}$$

If $\beta(x)$ is the solution of (3.22), then we prove $\beta(x) > 0$ on $[0, 1]$. First, suppose $\beta(x_0) = \min_{0 \leqslant x \leqslant 1} \beta(x) < 0$. Then noting the boundary condition of β, it is known that $x_0 \in (0, 1)$. Thus $\beta_{xx}(x_0) \geqslant 0$. But from (3.22) we have $d\beta_{xx}(x_0) = m(c_1 z - \beta(x_0))\,\beta(x_0) < 0$, which leads to a contradiction. So $\beta(x) \geqslant 0$. We further claim $\beta(x) \not\equiv 0$, otherwise it contradicts the boundary condition. If $\beta(x_1) = 0$ for some point $x_1 \in [0, 1]$, then $x_1 = 0$ or 1, otherwise $\beta(x) \equiv 0$, a contradiction. However, from the Hopf Boundary Lemma it follows that $x_1 \neq 0, 1$. This also gives a contradiction. Thus we have shown $\beta(x) > 0$ on $[0, 1]$.

It is easy to check that $\underline{\beta} = 0$, $\bar{\beta} = c_1 z$ are the ordered lower and upper solutions of (3.22). Thus in combination with $\beta > 0$ given above, there exists a solution β of (3.22) such that $0 < \beta \leqslant c_1 z$. Next we are going to show $\beta < c_1 z$. First we claim $\beta \not\equiv c_1 z$. If not, it gives a contradiction to the boundary condition. Let $\beta^1 = c_1 z - \beta$. Then $c_1 z > \beta^1 \geqslant 0 \not\equiv 0$, and

$$\begin{aligned} &d\beta^1_{xx} + m\beta^1(c_1 z - \beta^1) = 0, \\ &\beta^1_x(0) = 1 - c_1, \qquad \beta^1_x(1) + \gamma\beta^1(1) = 0. \end{aligned}$$

Suppose $\beta^1(x_2) = 0$ for some point $x_2 \in [0, 1]$. Then by the boundary condition we know $x_2 \neq 0$. If $x_2 \in (0, 1)$, it follows that $\beta^1 \equiv 0$, a contradiction. Finally, $x_2 = 1$. By the Hopf Boundary Lemma we obtain $\beta^1_x(1) < 0$, which leads to $\beta^1_x(1) + \gamma\beta^1(1) < 0$, a contradiction. So we conclude that $\beta^1 > 0$, i.e., $\beta < c_1 z$. Thus, it follows from the Comparison Theorem and (3.22) that $0 < \beta < z$.

If β_1 and β_2 represent the minimal and maximal solutions of (3.22) which are given by the monotone iteration from the above lower and upper solutions, then $0 < \beta_1 \leqslant \beta_2 < z$. Let $\hat{\beta} = \beta_2 - \beta_1$. Then $\hat{\beta} \geqslant 0$ and

$$\begin{aligned} &d\hat{\beta}_{xx} - m(c_1 z - \beta_1 - \beta_2)\,\hat{\beta} = 0, \\ &\hat{\beta}_x(0) = 0, \qquad \hat{\beta}_x(1) + \gamma\hat{\beta}(1) = 0. \end{aligned}$$

Since $c_1 z - \beta_1 - \beta_2 > (c_1 - 2) z \geqslant 0$, we know that $\hat{\beta} \equiv 0$. Hence $\beta_1 \equiv \beta_2$, which implies the uniqueness of positive solution of (3.22), denoted by $\beta^*(x)$.

Noting $0 = \underline{\beta} \leqslant \beta_0(x) \leqslant \bar{\beta} = c_1 z$, it follows from Ref. [24] that the solution of (3.21) satisfies $\lim_{t \to \infty} \beta(x, t) = \beta^*(x)$ uniformly for $x \in [0, 1]$.

With minor modification, we can proceed as above to prove that $R(x, t) \geqslant \tilde{\beta}(x, t)$ for $x \in [0, 1]$, $t > 0$, and $\lim_{t \to \infty} \tilde{\beta}(x, t) = \tilde{\beta}(x)$ uniformly for $x \in [0, 1]$, where $\tilde{\beta}(x, t)$ satisfies

$$\begin{aligned} &\tilde{\beta}_t = d\tilde{\beta}_{xx} - n((c+1) z - \min(c, 1) \tilde{\beta}) \tilde{\beta}, \\ &\tilde{\beta}_x(0, t) = -1, \qquad \tilde{\beta}_x(1, t) + \gamma \tilde{\beta}(1, t) = 0, \\ &\tilde{\beta}(x, 0) = \tilde{\beta}_0(x) \equiv R_0(x), \end{aligned}$$

and $\tilde{\beta}(x)$ is the unique corresponding positive steady-state solution.

In conclusion, there exist constants $\alpha_1 > 0$, $t_1 > 0$ such that $S(x, t) \geqslant \alpha_1$, $R(x, t) \geqslant \alpha_1$ for $x \in [0, 1]$, $t \geqslant t_1$. This completes the proof.

Let $s(x, t) = z - S(x, t)$, $r(x, t) = z - R(x, t)$. Then (s, r) satisfies

$$s(x, t) < z, \quad r(x, t) < z, \quad s(x, t) + cr(x, t) > 0 \qquad \text{for} \quad x \in [0, 1], \quad t > 0, \tag{3.23}$$

and

$$\begin{aligned} s_t &= ds_{xx} + m(s + cr) f(z - s, z - r), \\ r_t &= dr_{xx} + n(s + cr) g(z - s, z - r) \end{aligned} \tag{3.24}$$

with boundary conditions

$$\begin{aligned} s_x(0, t) &= 0, \qquad & r_x(0, t) &= 0, \\ s_x(1, t) + \gamma s(1, t) &= 0, \qquad & r_x(1, t) + \gamma r(1, t) &= 0 \end{aligned} \tag{3.25}$$

and initial conditions

$$s(x, 0) = s_0(x) = z - S_0(x), \qquad r(x, 0) = r_0(x) = z - R_0(x). \tag{3.26}$$

The main theorem concerning the longtime behavior is stated below with respect to (3.24)–(3.26). It can be easily restated with respect to the original system (3.17)–(3.19). Let $M = [s_1, s_2] \times [r_1, r_2]$, where (s_i, r_i) $(i = 1, 2)$ is given in the proof of Lemma 3.6.

THEOREM 3.15. *Suppose* $\min(m, n) > \hat{\lambda}_0$. *Then* M *is globally attracting for system* (3.24)–(3.26), *where* $\hat{\lambda}_0$ *is defined in Lemma* 3.13.

Proof. (i) Suppose $S_0(x) \leqslant z$, i.e., $s_0(x) \geqslant 0$. Then it follows from (3.23)(3.24) and the Maximum Principle that $s(x, t) > 0$ for $t > 0$. Similarly, $r(x, t) > 0$ if $R_0(x) \leqslant z$ for $t > 0$. Thus if $(S_0, R_0) \leqslant (z, z)$, there exists $\delta_0 > 0$ small enough such that

$$(\delta\phi, \delta\phi) = (\underline{s}, \underline{r}) \leqslant (s(x, \delta_0), r(x, \delta_0)) < (\bar{s}, \bar{r}) = (z, z).$$

By application of the monotone method [25] for the quasi-monotone system, it follows that the conclusion of this theorem holds in this case.

(ii) Suppose that $(S_0(x), R_0(x)) \leqslant (z, z)$ does not hold. For simplicity, we focus on the case that $S_0(x_0) > z(x_0)$ for some point $x_0 \in [0, 1]$ and $R_0(x) \leqslant z$ for $x \in [0, 1]$. The other two cases can be proved similarly with minor modifications. Since $\min(m, n) > \hat{\lambda}_0$, it follows from Lemma 3.13–3.14 that there exists $T_0 = \max(t_0, t_1)$ such that for $x \in [0, 1]$, $t \geqslant T_0$,

$$s \leqslant z - \alpha_1, \qquad r \leqslant z - \alpha_1, \qquad \text{and} \qquad s + cr \geqslant \alpha_0. \tag{3.27}$$

If $s(x, T_0) \geqslant 0$, by noting $r(x, t) > 0$ for $t > 0$, we can proceed as (i) to show that it can be done by choosing $(s(x, T_0 + \delta_0), r(x, T_0 + \delta_0))$ as initial value.

If $s(x, T_0) < 0$ for some point $x \in [0, 1]$, we make the change of variable $\hat{s}(x, t) = s(x, t) + \varepsilon z$ for any small $\varepsilon > 0$. Then

$$\begin{aligned} &\hat{s}_t = d\hat{s}_{xx} + F(\hat{s}, r), && 0 < x < 1, \quad t > T_0, \\ &\hat{s}_x(0, t) = -\varepsilon, \qquad \hat{s}_x(1, t) + \gamma\hat{s}(1, t) = 0, && t > T_0, \\ &\hat{s}(x, T_0) = \hat{s}_0(x) = s(x, T_0) + \varepsilon z, && 0 < x < 1, \end{aligned}$$

where

$$F(\hat{s}, r) = m(\hat{s} - \varepsilon z + cr)\, f(z - \hat{s} + \varepsilon z, z - r) \equiv m(s + cr)\, f(z - s, z - r).$$

From the definition of $\hat{s}(x, T_0)$ and $s(x, T_0)$, we know that there exists $\tau > 0$ such that $\hat{s}(x, T_0) \geqslant -\tau$. By the same technique below we can prove $\hat{s}(x, t) \geqslant -\tau$ for $t > T_0$.

Suppose that $0 < \tau' \leqslant \tau$ and there exists $(\hat{x}, \hat{t})$ $(\hat{t} \geqslant T_0)$ such that $\hat{s}(x, t) \geqslant -\tau'$ for $x \in [0, 1]$, $t < \hat{t}$, and $\hat{s}(\hat{x}, \hat{t}) = -\tau'$. Then by the boundary condition of $\hat{s}$, it is easy to know $\hat{x} \in (0, 1)$. Thus $\hat{s}_{xx}(\hat{x}, \hat{t}) \geqslant 0$. It follows from (3.23)(3.27) that

$$F(\hat{s}, r) > m\alpha_0 \frac{\alpha_1}{1 + a\alpha_1 + b\left(1 + \dfrac{1}{c}\right) z} \geqslant \eta > 0,$$

where $\eta = m\alpha_0\alpha_1\gamma/(\gamma(1+a\alpha_1)+b(1+\frac{1}{c})(1+\gamma))$. $r > -\frac{1}{c}s > -\frac{1}{c}z$ is used in the above argument. Hence the equation for $\hat{s}$ leads to

$$\hat{s}_t(\hat{x}, \hat{t}) = d\hat{s}_{xx}(\hat{x}, \hat{t}) + F(\hat{s}(\hat{x}, \hat{t}), r(\hat{x}, \hat{t})) \geqslant F(\hat{s}(\hat{x}, \hat{t}), r(\hat{x}, \hat{t})) > \eta > 0,$$

which gives $\hat{s}(\hat{x}, \hat{t}+h) > -\tau' + \eta h$ for $0 < h \ll 1$. Therefore, there is a neighbourhood of $\hat{x}$, denoted by $N(\hat{x})$ ($\subset (0, 1)$), such that $\hat{s}(x, \hat{t}+h) > -\tau' + \eta h$ for $x \in N(\hat{x})$, $0 < h \ll 1$. Let $\Gamma = \{x \in (0, 1) : u(x, \hat{t}) = -\tau'\}$. Then Γ is compact. By what we have just shown, there is an open set $\mathcal{O}$: $\Gamma \subset \mathcal{O} \subset (0, 1)$ such that for $x \in \mathcal{O}$, $0 < h \ll 1$, $\hat{s}(x, \hat{t}+h) > -\tau' + \eta h$. If $x \subset [0, 1] \backslash \mathcal{O}$, then we know from the definition of $\mathcal{O}$ that $\hat{s}(x, \hat{t}) > -\tau' + \delta_1$ for some small constant $\delta_1 > 0$. So $\hat{s}(x, \hat{t}+h) > -\tau' + \eta h$ for $x \in [0, 1] \backslash \mathcal{O}$, $0 < h \ll 1$.

In conclusion, there exists $h_0 > 0$ such that $\hat{s}(x, \hat{t}+h) > -\tau' + \eta h$ for $x \in [0, 1]$, $0 < h < h_0$. By iterating the above inequality N times, we find $\hat{s}(x, T_0 + Nh) > -\tau + N\eta h$ for $x \in [0, 1]$, $0 < h < h_0$. If $-\tau + N\eta h \geqslant 0$, i.e., $N \geqslant \frac{\tau}{\eta h}$, then we have $\hat{s}(x, T_0 + Nh) > 0$. Setting $N = [\frac{\tau}{\eta h}] + 1$, $T = T_0 + Nh$, we know that $\hat{s}(x, T) > 0$ for $[0, 1]$, where $[a]$ denotes the largest integer part not exceeding a. This gives $s(x, T) > -\varepsilon z$ for $x \in [0, 1]$. Letting $\varepsilon \to 0$, we have $s(x, T) \geqslant 0$ for $x \in [0, 1]$. Noting $r(x, T) > 0$, and taking $(s(x, T+\delta_0), r(x, T+\delta_0))$ as initial value, we can complete the proof as above.

By the definition of M, Theorem 3.15 gives uniform persistence [29].

COROLLARY 3.16. *Suppose* $\min(m, n) > \hat{\lambda}_0$. *Then the solution* (s, r) *of* (3.24)–(3.26) *is uniformly persistent.*

If $(s_1, r_1) = (s_2, r_2)$, i.e., the system (3.3)(3.4) has a unique positive solution, denoted by (s^*, r^*), where (s_i, r_i) $(i = 1, 2)$ is defined in the proof of Lemma 3.6, then we find that $M = (s^*, r^*)$ is globally attracting if $\min(m, n) > \hat{\lambda}_0$.

COROLLARY 3.17. *Suppose that* $\min(m, n) > \lambda_0/(1+c)$ *and one of the following three cases holds*: (i) $bm = acn$; (ii) $bm > acn$ *and* $1 + \frac{1}{\gamma} \leqslant \frac{nc}{bm - acn}$; (iii) $bm < acn$ *and* $1 + \frac{1}{\gamma} \leqslant \frac{m}{acn - bm}$. *Then* (3.3)(3.4) *has a unique positive solution. Moreover,* $M = (s^*, r^*)$ *is globally attracting if* $\min(m, n) > \hat{\lambda}_0$.

Proof. Following the proof of Lemma 3.6, we know that $(0, 0) < (s_1, r_1) \leqslant (s_2, r_2) < (z, z)$, and (s_i, r_i) $(i = 1, 2)$ satisfies

$$ds_{ixx} + m(s_i + cr_i)\, f(z - s_i, z - r_i) = 0,$$

$$dr_{ixx} + n(s_i + cr_i)\, g(z - s_i, z - r_i) = 0.$$

Suppose $(s_2, r_2) \not\equiv (s_1, r_1)$. Then we claim that $s_2 \not\equiv s_1$, $r_2 \not\equiv r_1$. If not so, say, $r_2 \equiv r_1$, it is easy to check from the equations of r_i $(i=1,2)$ that $s_2 \equiv s_1$, a contradiction.

Let $w = (s_2 + cr_2)/(s_1 + cr_1)$. Then w satisfies

$$dw_{xx} + 2d\frac{s_{1x} + cr_{1x}}{s_1 + cr_1} w_x + C(x)\, w = 0,$$
$$w_x(0) = 0, \qquad w_x(1) = 0,$$

where

$$\begin{aligned} C(x) &= mf(z-s_2, z-r_2) + cng(z-s_2, z-r_2) - mf(z-s_1, z-r_1) \\ &\quad - cng(z-s_1, z-r_1) \\ &= -\frac{[(m + (bm - acn)(z-r_1))(s_2 - s_1) + (cn - (bm - acn)(z-s_1))(r_2 - r_1)]}{(1 + a(z-s_2) + b(z-r_2))(1 + a(z-s_1) + b(z-r_1))}. \end{aligned}$$

It is known that $C(x) \leqslant 0$, $\not\equiv 0$ for each of the three cases. From the Maximum Principle we have $w \equiv 0$, which gives a contradiction to $w \geqslant 1$. Hence we have $(s_2, r_2) = (s_1, r_1)$.

Remark 6. Suppose $\min(m, n) > \lambda_0/(1+c)$. If $bm = acn$ or for fixed $\gamma > 0$, $|bm - acn| \ll 1$, then the hypothesis of Corollary 3.17 is satisfied.

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